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NUTRIENT CYCLING AND VERTICAL STRUCTURE IN EVERGREEN-OAK FOREST

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ABSTRACT

Some general aspects on nutrient cycling, nutrient budgets and vertical structure in evergreen-oak forests are discussed, synthetizing part of results from a large study, continued at present, in two sites in Catalunya, NE Spain. Nutrient stocks and fluxes, nutrient budgets in a forested watershed and vertical distribution of chlorophyll are considered here as some of the more characteristic features in ecosystem organization and dynamics.

INTRODUCTION

This paper is merely an outline on several general aspects concerning the biogeochemical cycles in evergreen-oak forest, regarded as part of the results achieved after a wide-range four-year programme in which departments of three Spanish universities have cooperated. The whole of this programme, which has led to establish experimental stations and field laboratories in the Prades and Montseny sierras, NE of the Iberian Peninsula, undertakes the survey of the forest structure, the vertical layer distribution in relation to the input radiation, some aspects of the water economy together with an in-depth study on each of the major fluxes involved in the nutrient circulation and other collateral studies. As a matter of fact, this is virtually the first study undertaken in the ecology of mediterranean forests in Spain.

The location and main characteristics of our evergreen-oak forest are shown in Figure 1. At the Montseny station as well as in most of the Prades site the vegetation belongs to the *Cuerceto mediterraneo-montanum* type, and only in the lower side of the latter there is a community closer to the *Cuerchetum ilicis galloprovinciale* type. They are relatively young high density forest with rather low basal areas, the exploitation of which came to an end approximately about 40-50 years ago. From the structural point of view we just will point out that the relevance of leaf biomass is higher than that of the deciduous forest: we have found around 6-7 t/ha; a similar average weight has been found in the fallen leaves covering the soil, even though it was obviously more unevenly distributed.

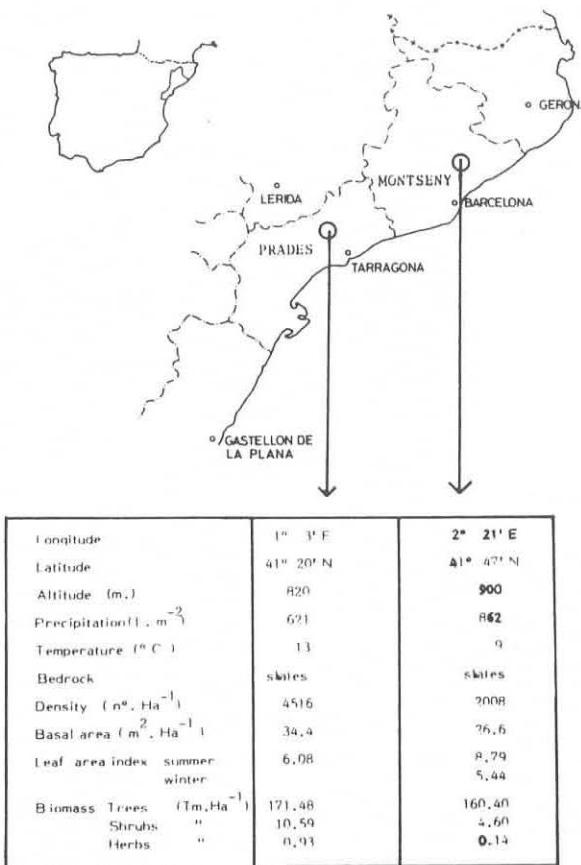


Figure 1. Location of the experimental stations and comparison of some major parameters.

NUTRIENT CYCLING

First of all we will show the results concerning the nutrient stocks and fluxes in the evergreen-oak forest at la Castanya, Montseny area (Figures 2 and 3). Our data, as a result of an average monitoring time ranging from three years in the majority of cases to one year in that of decomposition, show relevant differences in the cycles of the distinct elements, on one hand according to the different degree of mobility of each of them; and, on the other hand, to the different relative importance of each flux in relation to the vegetation requirements for its growth and for the production of the short turnover materials. A fundamental role seems to correspond to the translocation of nutrients. If concentration in leaves indicates the needs for nutrients, requirements seem not be very high: the average concentration of evergreen-oak leaves are generally lower than those of deciduous leaves. On the contrary, the higher quantities of leaves, half of them more than one year old, and the high concentration in twigs and thin wood, make the amount of elements in the biomass, considerably high. A great deal of nutrients like N, P and K are removed from leaves and twigs and transferred to other parts of the tree. In this way, low needs and high internal reserves constitute good adaptation in order to survive in poor and fluctuating environments.

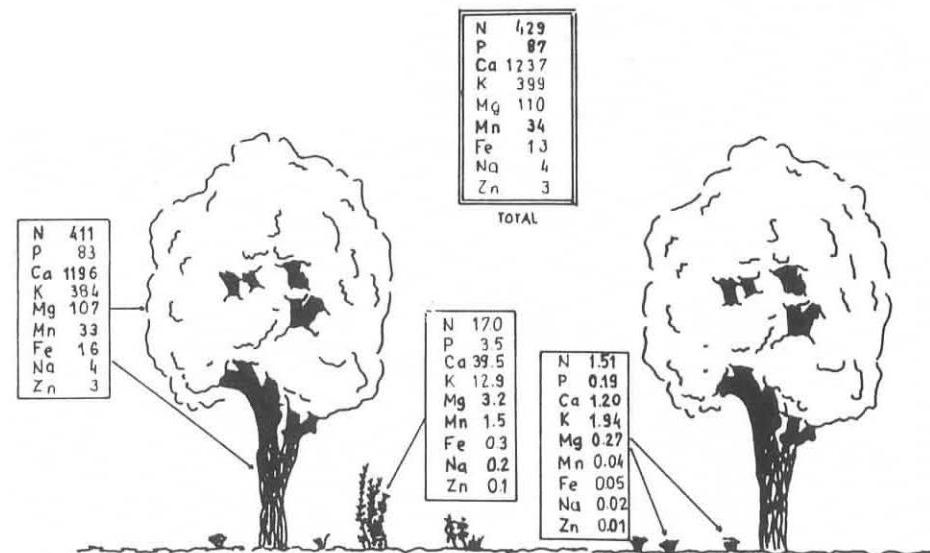


Figure 2. Distribution of nutrients in trees, shrubs and herbs of the evergreen-oak forest at la Castanya. All values in kg/ha.

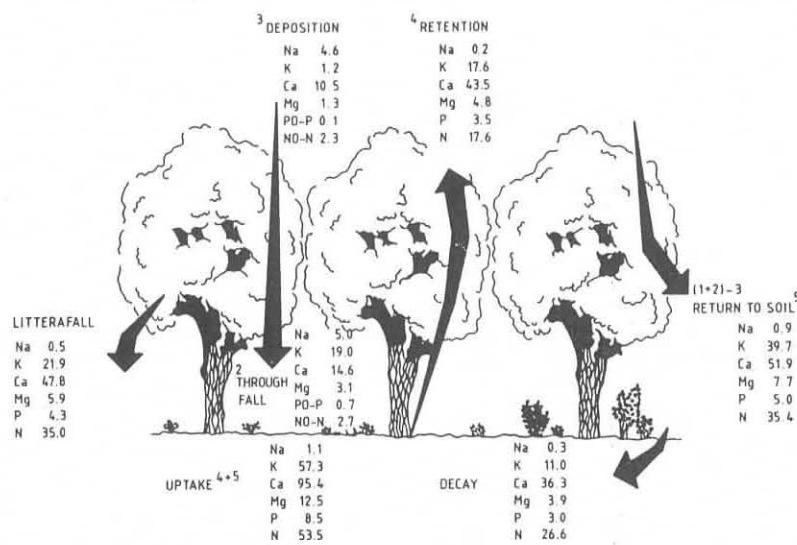


Figure 3. Annual cycle of Na, K, Ca, Mg, P and N at la Castanya. All values in kg/ha.

Table 1 shows both the circulation rates and turnover time for each of the different main elements. The data should be somewhat modified taking into account the fact that different fluxes have not been directly measured or are under/overestimated. Nevertheless, we consider that in such a case the order of elements would not be substantially modified.

Element	Circulation rate (years^{-1})	Time turnover (years)
Na	0.2	4.4
K	0.1	9.7
Ca	0.043	23.0
Mg	0.072	13.9
N (only in litter fall)	0.086	11.6
P	0.06	16.6

Table 1 - Circulation rates and time turnover of major elements

As a result of the available data we have come to the conclusion that the atmospheric input can actually compensate for the yearly accumulation of N, Ca, and Mg, measured as the total amount in biomass for each element divided by forest age; in the case of K, the atmospheric input only amounts from 1/4 to 1/5 for its requirements, therefore, the role of weathering can be estimated to be more relevant in the case of this element.

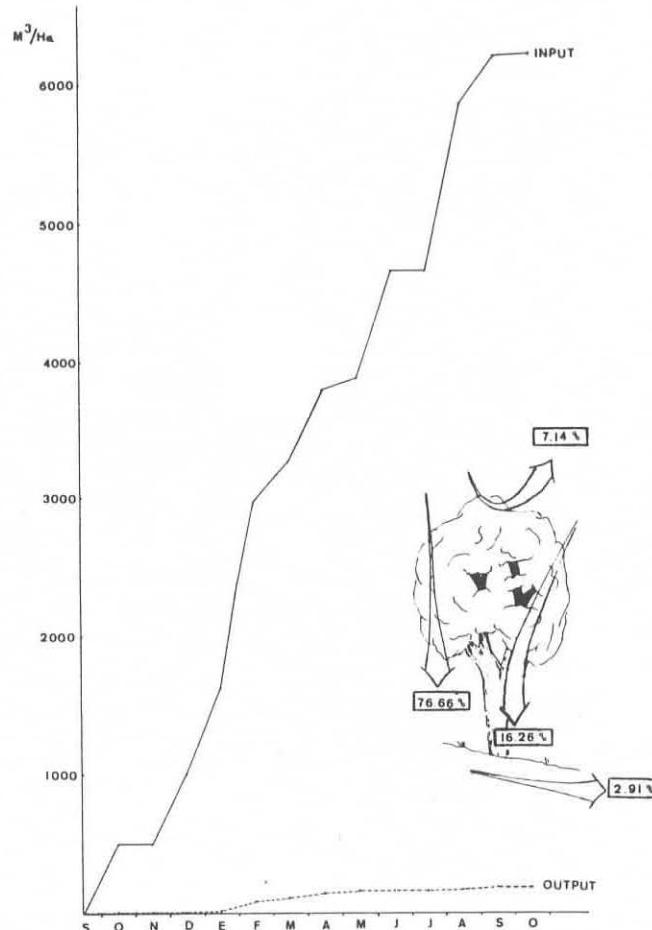


Figure 4. Water fluxes in the evergreen-oak forest and water budget in the forested watershed at Prades.

NUTRIENT BUDGETS

In the Prades experimental site the bedrock is basically formed by shales or granites, and some forested watersheds can be limited in the form of functional units with unpermeable substrata; water and nutrient budgets can be measured in this way (Likens et. al. 1977).

At present the water input and output, in only one of these watersheds, is being monitored. The volume and chemical composition in bulk precipitation throughfall, stemflow and stream water have been measured during a year. Figure 4 shows the percentage distribution of precipitation water; an outstanding value in stemflow and low degree of interception appears. The accumulated water input/output diagram shows a neat divergence due to the fact that total output amounts to ca. 3 % on the input.

Figure 5 shows nutrient fluxes in bulk precipitation, litter fall, net throughfall, net stemflow and stream water in dissolved form. Particulated matter is merely regarded as dry weight and is two orders of magnitude smaller than the estimated in Hubbard Brook (Bormann et. al. 1969).

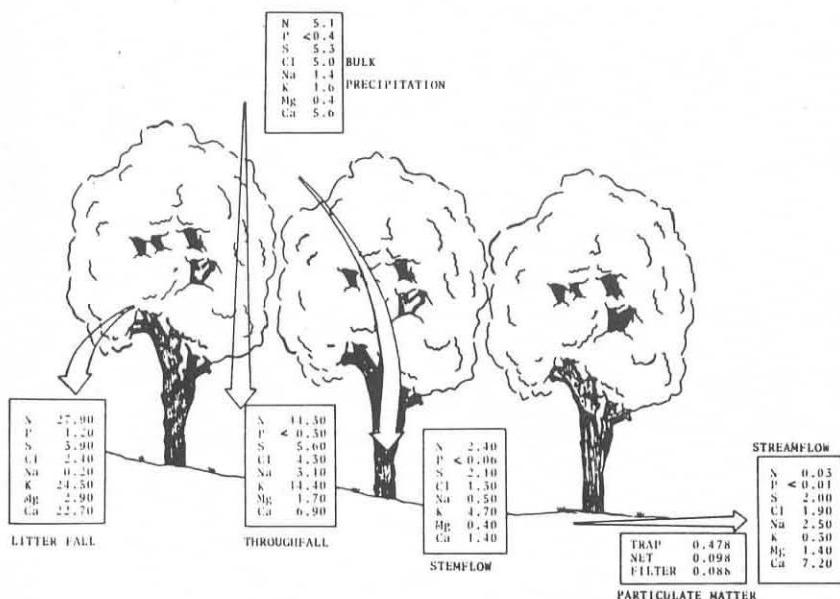


Figure 5. Nutrient fluxes in the evergreen-oak forest at Prades. All values in kg/ha.

Nutrient budgets are shown in Table 2 and corresponding input/output diagrams are displayed in figure 6. Input clearly exceeds output in NO_3^- , H^+ , NH_4^+ , K^+ , Cl^- , F^- and SO_4^{2-} , whereas in the cases of CO_3^{2-} , Na^+ , Ca^{2+} , and Mg^{2+} , output is higher than input.

	Input kg/ha.year	Output kg/ha.years	Budget
H^+	0.13	$0.0064 \cdot 10^{-3}$	+ 0.13
Na^+	1.95	2.47	- 0.52
K^+	1.63	0.35	+ 1.28
Ca^{2+}	5.61	7.25	- 1.64
Mg^{2+}	0.37	1.43	- 1.06
NH_4^+	4.59	0.03	+ 4.56
CO_3^{2-}	18.30	28.82	- 8.08
F^-	0.18	0.038	+ 0.14
Cl^-	5.03	1.92	+ 3.11
NO_3^-	6.54	-	-
SO_4^{2-}	15.97	6.18	+ 9.79

Table 2 - Annual input/output budgets for different ions

VERTICAL STRUCTURE

Aspects of the survey on which we have focused more attention are those of the variation in foliar morphology, pigments contents and transpiration behaviour alongside the forest's vertical profile. Vertical organization of forest is an essential feature. As an example we will make some remarks about vertical distribution of photosynthetic pigments, a relevant and not so frequently studied parameter.

The analysis of the vertical distribution of chlorophyll in the evergreen oak shows clearly a vertical structure with a maximum that divides the canopy into two layers: the top layer with a depth of about 1 meter and the lower layer which extends practically to the ground.

The average leaf surface of the upper layer is remarkably less than that of the lower layer which in accordance with Horn (1971) is interpreted as an adaption to conditions of high illumination.

Accumulation of materials is greater into leaves of higher levels. It can be explained if we consider that the transpiration of these leaves, subjected to high levels of solar radiation, is greater than that of those in the lower levels and this means a greater accumulation of organic matter and other materials in leaves.

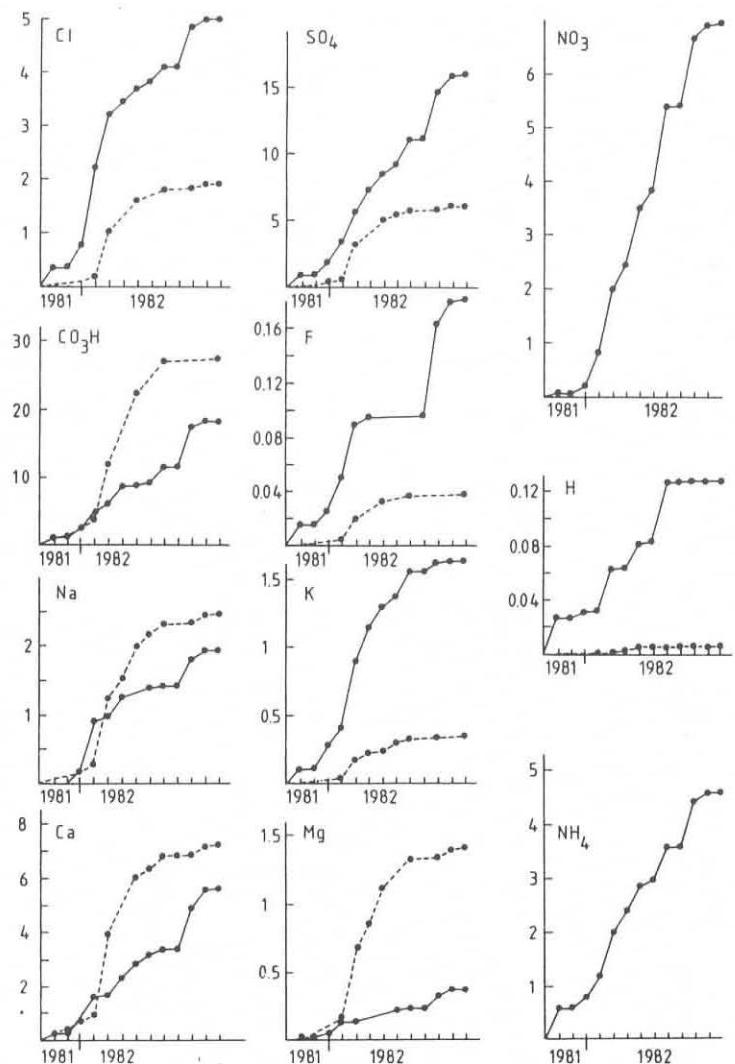


Figure 6. Nutrient budgets in the forested watershed at Prades. Solid lines are input and dashed lines are output. All values in kg/ha.

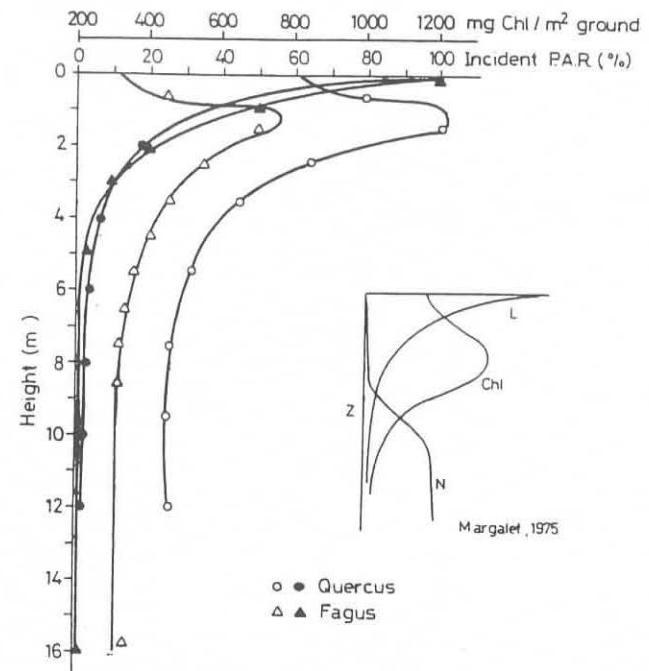


Figure 7. Vertical distribution of incident PAR (solid dots) and chlorophyll (open dots) in the evergreen-oak forest at la Castanya. Distribution of the same parameters in a beech forest (solid and open triangles), also in Montseny, is showed for comparison. Distribution of light (L), chlorophyll (Chl) and nutrients (N) in aquatic ecosystems are showed too.

The amount of chlorophyll in the uppermost level must be independent of the incident PAR, because photosystems are saturated. In leaves of lower layer, at which radiation has been reduced the amount of chlorophyll can be related closely to the intensity of incident PAR. The result is a vertical distribution with a maximum similar to the characteristic distribution of aquatic ecosystems (Margalef 1974) represented in figure 7.

We can try to explain accumulation of leaves in the top of canopy. Competition for light favours probably this type of distribution. Accumulation of leaves at the top of canopy introduce a delay in the circulation of nutrients as the distance between roots and canopy increases. This leads to a most parsimonious use of the energy by forest.

Leaves at the surface, smaller in size, make sense only where the proportion of incident photons is high and photosystems have a greater chance of being

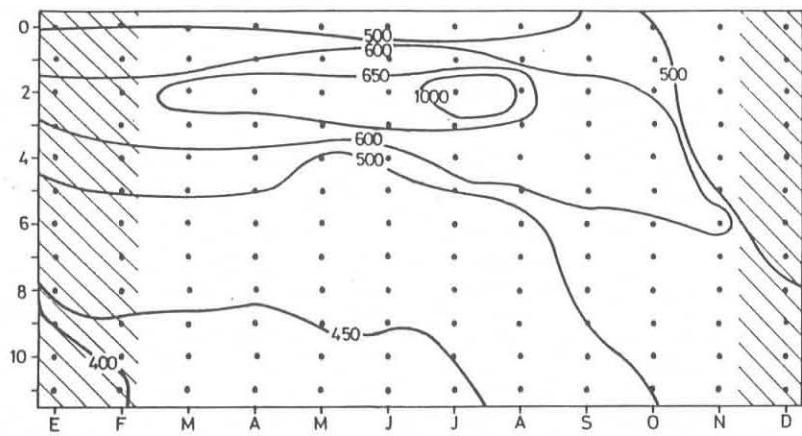


Figure 8. Annual evolution of vertical distribution of chlorophyll(a+b) in the evergreen-oak forest at la Castanya.

reached, at time that represents the possibility of having more leaf area exposed to intense light without producing an excessive reduction of illumination. As we descend from the top, and the radiation becomes less intense it makes no sense having so much chlorophyll (a molecule metabolically expensive) since the probability that its active centres will be reached by photons is reduced. It would be more interesting to have larger leaves to ensure the possibility of intercepting light. It is so important to "extend" chlorophyll as to increase it.

In any ecosystem one can see a trend in the sense of increasing the production per unit of invested energy. In aquatic ecosystems, the surface layer of water is the most productive. In forest, the production of uppermost layer is also higher because forest has there half its leaf area and more than half of its chlorophyll.

Vertical distribution of chlorophyll is also a dynamic property of forests and it is related to the amount of incident PAR reaching canopy. Figure 8 shows annual changes with a summer maximum. We can see in all these facts some parallelisms with aquatic ecosystems.

ACKNOWLEDGEMENT

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